

THE IMPACT OF TIMBER MANAGEMENT ON THE PHYTOCHEMICALS ASSOCIATED WITH BLACK BEAR DAMAGE

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ABSTRACT: Black bears forage on Douglas-fir vascular tissue in the spring, and this behavior can be severely detrimental to the health and economic value of a timber stand. Foraging is selective in that not all stands are damaged and, within a stand, one tree may be stripped while its neighbor is ignored or minimally sampled. A series of studies was conducted to assess whether bear selectivity is affected by chemical constituents within vascular tissue, and whether these constituents are affected by silvicultural practices. The results are interpreted to identify forest practices that may alleviate damage, or at least predict where damage is most likely to occur.

KEY WORDS: Black bear, damage, fertilization, foraging, forest resources, genetics, pruning, sugars, terpenes, thinning

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INTRODUCTION

Black bears (*Ursus americanus*) commonly forage on Douglas-fir (*Pseudotsuga menziesii*) trees during the spring (Ziegltrum and Nolte 1996). Vascular tissues from Douglas-fir are staples in the diet of some bears (Noble 1993). Bears generally forage on the lower bole of trees, ranging from 15 to 30 years of age, by removing the bark with their claws and then scraping the vascular tissue from the heartwood with their incisors. Any age tree, however, is vulnerable to bear damage and bears occasionally strip an entire tree. Damage within a stand can be extensive as a single bear may peel bark from 50 to 70 trees per day (Schmidt and Gourley 1992).

The damage inflicted by bears is extremely detrimental to the health and economic value of a timber stand. Complete girdling is lethal, while partial girdling reduces growth rates and provides avenues for subsequent insect and disease infestations (Kanaskie et al. 1990). The severity of timber loss is compounded because bears tend to select the most vigorous trees within the most productive stands, and often damage occurs after stand improvements (e.g., thinning, fertilizer) have been implemented (Mason and Adams 1989; Nelson 1989; Kanaskie et al. 1990; Schmidt and Gourley 1992). The problem is exacerbated because of the extended time (20 plus years) necessary for a timber stand to return to its pre-damaged state.

Foraging bears appear to be selective in their choice of trees. Several trees within a stand may be stripped while their adjacent neighbors are ignored or minimally sampled. Bear damage also occurs more frequently in certain types of timber stands. Thinned stands tend to be more vulnerable than higher density stands (Mason and Adams 1989; Kanaskie et al. 1990; Schmidt and

Gourley 1992). Depredation also has been reported to increase after fertilization (Nelson 1989). The apparent dietary criteria of bears is to select for vigorous trees.

This paper summarizes a series of studies conducted to assess whether bear selectivity is affected by chemical constituents within vascular tissue, and the impact of forest management practices on these constituents.

RELATIONSHIP OF CHEMICAL CONSTITUENTS AND BEAR FORAGING

The authors related damage to the concentration of sugars and terpenes found in the vascular tissue of Douglas-fir. Sugars were chosen because of their high concentration in vascular tissue (Radwan 1969). Animals derive energy or protein from the plants they ingest (Robbins 1983). There is little or no protein in Douglas-fir vascular tissue (Radwan 1969). Therefore, the benefit bears glean from Douglas-fir must be obtained from the energetic sugars. Other omnivores, such as rats, demonstrate a preference for foods containing sugars (Jacobs et al. 1978).

Terpenes were investigated because high concentrations are present in conifers (Kimball et al. 1995), and they deter foraging by other species. Pine oil repels snowshoe hares (*Lepus americanus*) and voles (*Microtus townsendii*) (Bell and Harestad 1987) and causes avoidance behavior in pocket gophers (*Geomys bursarius*) (Epple et al. 1996). Several terpene compounds in balsam poplar deter feeding by snowshoe hares (Reichardt et al. 1990). The concentration of certain monoterpenes also is a predictor of tassel-eared squirrel (*Sciurus aberti*) feeding on ponderosa pine (*Pinus ponderosa*) (Farentinos et al. 1981).

Chemical Constituents

The initial study correlated chemical constituents in Douglas-fir trees to the extent of damage inflicted by black bears (Kimball et al. 1998b). Stands of Douglas-fir were monitored for bear foraging activity during the spring of 1994 and 1995. Stands with recent (less than five days) damage to at least 15 trees were included in the study. Only Douglas-fir trees with areas of removed bark and incisor marks on the remaining vascular tissue were sampled. Trees with no evident foraging marks were not sampled since it could not be ascertained whether they had been encountered by a foraging bear.

The surface area or removed bark and diameter at breast height (DBH) were determined for each damaged tree. Vascular tissue was collected by removing two 40 x 10 cm patches of bark on opposite sides of the tree and scraping the vascular tissue (phloem and xylem oleoresin located immediately beneath the cork cambium) into a freezer bag. Samples were collected at breast height (1.5 m).

The freezer bag and contents were immediately placed in liquid nitrogen for two to five minutes. The samples were kept frozen until homogenized with a mallet and divided into two portions. One portion was maintained frozen until analyzed for terpenes, while the other was lyophilized and analyzed for carbohydrates. Chemical analyses for terpenes (Kimball et al. 1995) and carbohydrates (Kimball et al. 1998b) are described elsewhere. Vascular tissue density was determined as the mass of vascular tissue per 800 cm² sample area.

Douglas-fir vascular tissue was analyzed for 20 different terpenes. Typically, the most prevalent terpene compounds were: alpha-pinene, beta-pinene, sabinene, limonene, 3-carene, myrcene, camphene, terpinolene, and bornyl acetate (in order of abundance). The concentration of alpha-pinene was approximately ten times that of the other major terpenes. Galactose, glucose, xylose, fructose, sucrose, coniferin, and an unknown compound were present in all extracts analyzed for sugars.

For statistical analysis, the variables were: concentration of hydrocarbon monoterpenes, concentration of oxygenated monoterpenes, concentration of sesquiterpenes, concentration of major carbohydrates, concentration of coniferin, vascular tissue density, and DBH.

Multiple regression yielded significant models for four of the six sites (Table 1). The coefficients of determination (R^2) obtained from the significant models indicate that the variables used account for half to three-quarters of the variation observed in the removed bark data. Diagnostic evaluation of the data detected no violations of the assumptions of linear regression.

The results indicated that tree selection by bears is probably related to sugars and terpenes. Bears select for sugars and select against terpenes. It is assumed that the amount of bark removed from a tree was directly related to bear preference for that tree. Trees with minimal (ca. 20 cm²) bark removed during foraging were frequently found adjacent to trees with extensive (up to 15,500 cm²) bark damage. The area of bark removed was the only quantitative evidence of preference present. Therefore, trees with minimal bark damage were regarded as less preferred trees. While highly preferred trees were those

with extensive bark removal. The correlative nature of this study, however, did not establish that the chemical constituents were causally related to preference.

Bear Bioassays

The field bioassay was designed to establish causative effects on foraging preference due to sugars and terpenes (Kimball et al. 1998b). Free ranging black bears were offered the choice of four prepared test diets varying in carbohydrate and terpene concentrations (Table 2). Diet delivery was based on the supplemental feeding program of the Washington Forest Protection Association (WFPA; Ziegler and Nolte 1996).

Ten sites with a history of bear activity were selected for the study. At each site, four feeders were placed in close proximity (10 cm) to each other in a square configuration with the feeder openings oriented toward a central focus. A pre-bait treatment was conducted to entice bears to the stations and to ensure adequate activity. The pre-bait treatment consisted of filling each feeder with the supplemental feed employed by the WFPA feeding program and hanging a beaver carcass in a tree near the feeding stations. Sites were monitored for activity every third or fourth day. Two sites were eliminated from the study because of low bear activity.

Following two weeks of bear activity at a site, the WFPA feed was removed and the four test diets were randomly placed in the feeders. Sites were monitored every three or four days for a total of seven monitoring intervals. Mean daily intake was calculated for each interval.

Bears selected diets to regulate their intake of carbohydrates and terpenes (Figure 1). The free ranging bears in this study preferred the low terpene diets to the high terpene diets at the high sugar concentration. Bears also preferred the high sugar/high terpene diet to the low sugar/high terpene diet. Generally, sugars produce positive feedbacks from intake while terpenes can induce negative consequences. Thus, bears appear to have learned to forage in a manner that maximizes sugar intake while minimizing terpene intake.

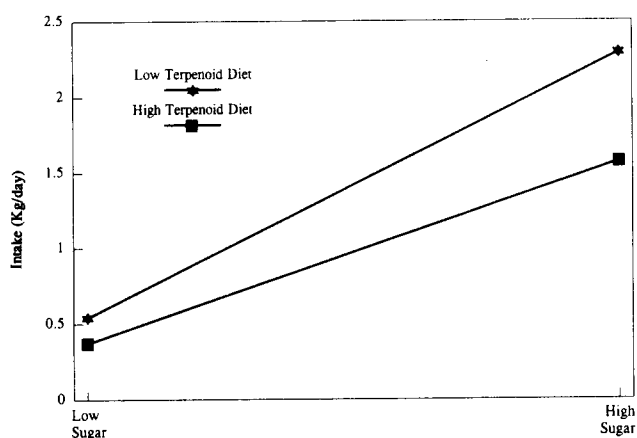


Figure 1. Mean daily intake of the four test diets used in the bioassay to assess bear responses to varying concentrations of sugars and terpenes (Kimball et al. 1998b).

Table 1. Statistics from multiple regression analyses where area of removed bark was the response and the predictors were the chemical concentrations of hydrocarbon monoterpenes, oxygenated monoterpenes, sesquiterpenes, carbohydrates, and coniferin, and the physical measurements tree diameter (DBH) and vascular tissue density (Kimball et al. 1998b).

Statistics	Site					
	McCleary	Kelso	Cowlitz	Raspberry	Silver Falls	Molalla
p	0.80	0.05	0.06	0.04	0.60	0.03
R ²	0.14	0.44	0.78	0.63	0.44	0.55

Table 2. Concentrations of carbohydrates and terpenes in diets offered to black bears during field bioassays.

Diets	Carbohydrates	Terpenes
High Sugar/High Terpene	8.5%	263 ppm
High Sugar/Low Terpene	8.0%	86 ppm
Low Sugar/High Terpene	5.0%	290 ppm
Low Sugar/Low Terpene	5.0%	44 ppm

IMPACT OF FOREST MANAGEMENT PRACTICES

The next series of studies investigated the impact of forest management practices on the chemical constituents identified as affecting bear behavior. The authors wanted to determine whether their foraging model could help to identify forest practices that may alleviate damage, or at least to predict where damage is most likely to occur. Stand density was selected because it is generally understood that bear damage is likely to increase in a thinned stand (Mason and Adams 1989; Kanaskie et al. 1990; Schmidt and Gourley 1992). Thus, investigating changes in chemical constituents relative to stand density provided an opportunity to assess whether the predictor of damage compared favorably with common knowledge. Similarly, the authors wanted to ascertain whether their model matched favorably with what was known regarding an increase in bear damage post urea fertilization (Nelson 1989).

Bear response to pruned trees was largely unknown. After determining the effect pruning had on vascular tissue concentrations of sugars and terpenes, the authors were fortunate to have the opportunity to evaluate bear damage within stands where every other tree had been pruned. Finally, chemical concentrations among progeny test families were evaluated to determine the potential of selecting for a tree less palatable to wildlife while maintaining desirable qualities, such as productivity.

Thinning and Fertilization

For this study, it was hypothesized that bear preference for trees in thinned or fertilized stands was mediated by a higher concentration of vascular sugars and/or a lower terpene concentrations relative to trees in higher density or unfertilized stands (Kimball et al. 1998d).

The study was conducted on Stand Management Cooperative (SMC) installations in western Washington and Oregon. SMC installations were established in healthy Douglas-fir stands planted between 1974 and 1984. The cooperative initiated silvicultural treatments between 1987 and 1992 to investigate the impacts of current management practices on growth and wood production (Stand Management Cooperative 1993). The SMC employed pre-commercial thinning to yield three stand density levels. High density plots (850 to 1,400 stems per hectare; sph) were obtained by not thinning, while other plots were thinned to a mid-density level (400 to 700 sph), and yet other plots were thinned to a low density level (250 to 325 sph). Trees on fertilized and unfertilized plots representing each of these density levels were investigated. Urea (46-0-0) had been hand applied (224 kg/ha) 1, 2, 3, or 4 years prior to sampling.

Growth parameters were measured and tissue samples were collected from eight trees within each plot. Sample collection was as previously described, except a single 80 cm x 10 cm patch was taken from the east side of the tree. Samples were stored, and the chemical assays to determine sugar and terpene concentrations were conducted as described by Kimball et al. (1995) and Kimball et al. (1998b).

Tree diameter (a measure of cumulative growth; Table 3) and vascular tissue mass (a measure of current growth; Figure 2) were increased by thinning. Furthermore, thinning significantly increased the sugar concentration of the vascular tissue (Table 3) while having only a minor impact on the terpene concentration. Thus, the net effect of thinning was an increase in the sugar to terpene ratio of the vascular tissue.

Table 3. Mean tree diameters ($p = 0.007$) and vascular tissue sugar concentration ($p = 0.02$) by tree density level (values followed by the same letter are not significantly different; Kimball et al. 1998d).

Density Level	Tree Diameter	Total Sugar Concentration
Low (250 to 325 sph)	20.4 cm (A)	3.19% (A)
Mid (400 to 700 sph)	18.9 cm (B)	3.03% (B)
High (850 to 1,400 sph)	18.1 cm (B)	2.98% (B)

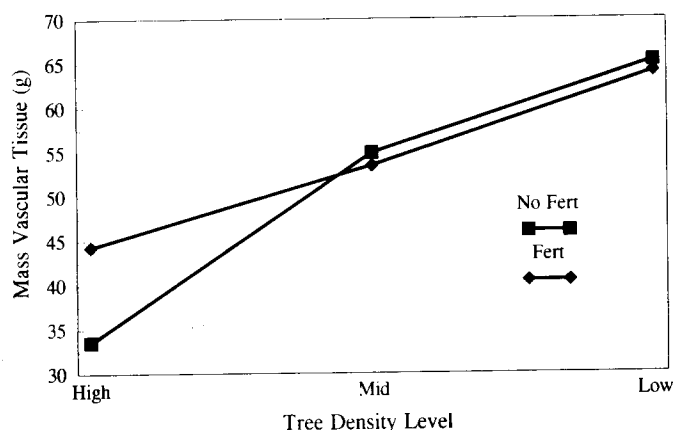


Figure 2. Effects of tree density and fertilization on vascular tissue mass (Kimball et al. 1998d).

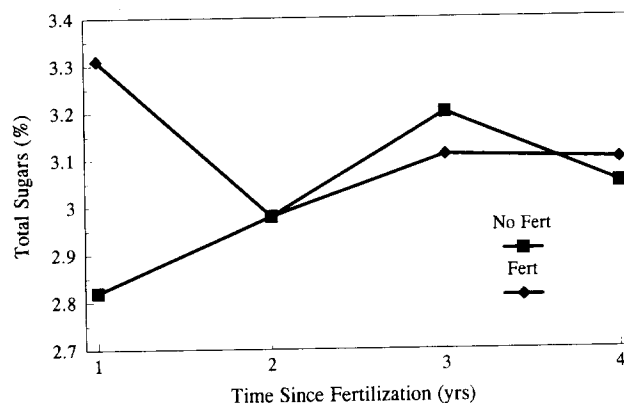


Figure 3. Effects of urea fertilization and time since fertilization on total sugars (Kimball et al. 1998d).

Fertilization had a positive effect on DBH. Sugar concentration was impacted only the first year after fertilizing (Figure 3), and there was no impact on terpenes. Fertilization had a positive effect on tissue mass in high density stands, but did not have an effect at mid or low density levels (Figure 2). Though trees were not sampled the year fertilizer was applied, it is likely that fertilization effects were apparent the year of treatment. Uptake of nitrogen by conifers can be rapid (Carlyle 1995). The observed increase in tree diameter in the absence of increased vascular tissue mass suggests a growth spurt in the same year the treatment was applied. There was no difference in sugars between trees on fertilized and unfertilized plots after the first year.

These results provide credence to the hypothesis that the concentration of chemical constituents within forage can be used to predict the occurrence of bear foraging. Bear preference for trees in thinned stands may be partially attributed to higher vascular tissue sugar concentrations. Bears also benefit by foraging where the available mass of vascular tissue is greater, most likely providing more return per bite.

Bear preference for fertilized stands also can be explained, at least in part, by the chemical constituents of the vascular tissues. Nelson (1989) indicated that bear damage in fertilized stands was most frequent in the years immediately after fertilization. Results suggest that bears prefer urea fertilized trees the spring after treatment, and this preference probably last through the next year.

Pruning

Pruning is typically performed to increase wood quality (O'Hara 1991), but it also can negatively impact tree growth (Langstrom and Hellqvist 1991). The authors hypothesized that pruning also would impact the chemistry of the vascular tissue, perhaps rendering the trees less desirable to bears. This study was conducted to assess the affect of pruning on the concentrations of sugars and terpenes within the vascular tissue of Douglas-fir (Kimball et al 1998c). Subsequent to the chemical assays, the authors were fortunate to be able to test their prediction of bear foraging within stands where every other tree had been pruned.

The impact of live crown pruning on the allocation of sugars and terpenes in the vascular tissue was investigated on three Oregon Department of Forestry (ODF) sites. At each of these sites, two years prior to tissue sampling all the live and dead whorls were removed to a height of 5.0 m. This resulted in the removal of approximately 40% of the live crown.

Vascular tissue samples were collected as previously described, except samples were collected from three heights along the stem of the tree. First, a lower bole sample was collected at 1.0 m from the east side of a pruned tree. The mid bole sample was located at the point of the first whorl of live branches. The upper bole sample was taken half way between the mid bole sample and the top of the tree. Samples were then collected at the same locations from an adjacent unpruned tree, paired

because of similarities in height and diameter. Eight pairs of pruned and unpruned trees were sampled at each site. All samples were analyzed for sugars and terpenes as previously described.

Pruning significantly impacted growth and vascular chemistry throughout the bole of the tree (Table 4). Growth was suppressed in pruned trees, particularly in the lower bole. Vascular tissue mass and sugar concentrations also were reduced in pruned trees. Terpene concentrations were highest in the lower bole. Sesquiterpenes were the only group of terpenes to be affected by pruning. Sesquiterpene concentration in pruned trees was 0.37 ppm and 0.15 ppm in unpruned trees. Thus, pruning decreased the sugar to terpene ratio. The authors would predict, therefore, that pruned trees would be less desirable to bears than unpruned trees, particularly in the lower bole which is the part of the tree most likely to be encountered.

Bear preference for unpruned trees was demonstrated in a survey of bear damage on a 21 ha ODF site which had been subjected to the same pruning treatment as described above. Trees with existing bear damage at the time of treatment were marked by painting the damaged area. Treatment was applied four years prior to this survey. Bear damage was evaluated by recording the species, treatment (pruned or unpruned), bear damage since treatment (yes or no), and pre-treatment damage (paint or no paint) for all trees (1,646) that occurred within five, 15 m wide transects systematically placed across the site.

Species encountered in the survey were Douglas-fir (77%), Western hemlock (22%), and Sitka spruce (1%; *Picea sitchensis*). Presence of Sitka spruce was inadequate for statistical analysis. Pre-treatment damage occurred independent of treatment. Therefore, there was not a worker bias to select for a precondition (damaged or undamaged) while pruning. Damage since treatment was significantly impacted by pruning. The calculated odds ratio suggests that unpruned Douglas-fir trees were four times more likely to be damaged than pruned trees. Similarly, unpruned Western hemlock were three times more likely to be damaged than pruned trees. Providing further confidence in the hypothesis that bear foraging choices reflect chemical constituents.

Genetic Selection

Douglas-fir genetics has been previously related to mammalian herbivory. Foliar concentrations of monoterpenes in certain Douglas-fir clones are thought to render them less palatable to deer (Radwan and Ellis 1975). Similarly, snowshoe hare avoidance of Douglas-fir is under genetic control (Dimock 1976). This study was conducted to determine whether terpenes previously identified to affect bear foraging behavior are subject to genetic control (Kimball et al. 1998a).

The impact of progeny selection on the allocation of terpenes in the vascular tissue was investigated in a cooperative study with the USDA Forest Service and the Northwest Tree Improvement Cooperative. Samples were collected from six known genetic families of Douglas-fir at five different progeny test sites. These sites were originally established 28 year ago to rank families for growth and wood quality traits. Test families for this study were selected to provide comparisons among original growth rankings (taken at 15 years of age) from slow to fast growth. The DBH and mass of vascular tissue in the 800 cm² sampling area were determined as a measure of cumulative and current growth for each tree. Vascular tissue samples were collected and analyzed for terpenes according to the procedures of Kimball et al. (1995).

Tree diameter was consistent with the original rankings (Table 5). Mass of vascular tissue (current growth) was similar among families. Similarities in current growth may have been because canopy closure had induced self pruning causing a decrease in vascular tissue growth in the lower bole of the tree (Kimball et al. 1998c).

Chemical assays indicated that the amount of terpenes is not necessarily correlated with growth. Principle components analysis assigned related terpenes to five terpene groups, based on the correlation matrix. All terpenes within a group were positively correlated with each other. Terpenes in two of these groups were subject to site x family interactions. Some families had high concentrations at one site, but contained low concentrations at another site. In a third group of terpenes the concentrations of some individual terpenes were higher in faster growing families than in those

Table 4. Relative presence of vascular tissue chemical constituents of pruned and unpruned Douglas-fir trees at three bole heights ($P < 0.05$; Kimball et al. 1998c).

Chemical Constituent	Treatment	Bole Height
Vascular tissue mass	Unpruned > Pruned	Mid = High > Low
Hydrocarbon Monoterpenes	Unpruned = Pruned	Low > Mid = High
Oxygenated Monoterpenes	Unpruned = Pruned	Low > Mid = High
Sesquiterpenes	Pruned > Unpruned	Low > Mid = High
Total Carbohydrates	Unpruned > Pruned	Low = Mid = High

families with less growth potential. Interestingly, the terpenes in group 2 are in general the most prominent terpenes present in Douglas-fir vascular tissue. This relationship suggests that it may be possible to select for trees that are less palatable to bears without sacrificing growth potential.

SUMMARY

Tree selection by black bears is at least in part related to the concentrations of sugars and terpenes present in vascular tissue. Bears foraging in environments that offer choices are likely to select for trees which offer the

highest sugar to terpene ratio. This research suggests that the sugar to terpene ratio of Douglas-fir vascular tissue can be reduced by cultivating trees at higher stand densities and by pruning live crown cover. Urea fertilization affects the ratio only the initial couple of seasons after application. While sugar concentrations were affected by environmental factors, terpene concentrations can be increased through genetic selection. It appears plausible to select for trees containing greater concentrations of terpenes without affecting positive attributes such as productivity.

Table 5. Current mean DBH and original rank (15 years) of six genetic families of Douglas-fir at five different progeny test sites (DBH values followed by the same letter are not significantly different (Kimball et al. 1998a).

Family	Original Rank	Current DBH
21	4	25.25 A
90	1	24.39 AB
20	10	23.16 BC
29	13	23.11 BC
30	22	22.12 C
376	18	22.10 C

REFERENCES

- BELL, C. M., and A. S. HARESTAD. 1987. Efficacy of pine oil as repellent to wildlife. *J. Chem. Ecol.* 13:1409-1417.
- CARLYLE, J. C. 1995. Nutrient management in a *Pinus radiata* plantation after thinning: the effect of nitrogen fertilizer on soil nitrogen fluxes and tree growth. *Can. J. For. Res.* 25:1673-1683.
- DIMOCK, E. J., R. R. SILEN, and V. E. ALLEN. 1976. Genetic resistance in Douglas-fir damage by snowshoe hare and black-tailed deer. *For. Sci.* 22:106-121.
- EPPLE, G., H. NIBLICK, S. LEWIS, D. L. NOLTE, D. L. CAMPBELL, and J. R. RUSSELL. 1996. Pine needle oil causes avoidance behaviors in pocket gopher *Geomys bursarius*. *J. Chem. Ecol.* 22:1013-1025.
- FARENTINOS, R. C., P. J. CAPRETTA, R. E. KEPNER, and V. M. LITTLEFIELD. 1981. Selective herbivory in tassel-eared squirrels: role of monoterpenes in ponderosa pines chosen as feeding trees. *Science* 213:1273-1275.
- JACOBS, W. W., G. K. BEAUCHAMP, and M. R. KARE. 1978. Progress in animal flavor research. Pages 1-20 in *Flavor Chemistry of Animal Foods* (R. W. Bullard, ed.), American Chemical Society, Washington, DC.
- KANASKIE, A., J. CHETOCK, G. IRWIN, and D. OVERHUSLER. 1990. Black bear damage to forest trees in Northwest Oregon 1988-1989. Pest Management Report 90-1, Oregon Department of Forestry, Salem, OR.
- KIMBALL, B. A., R. A. CRAVER, J. J. JOHNSTON, and D. L. NOLTE. 1995. Quantitative analysis of the mono- and sesquiterpenoids of Douglas-fir tissue by solvent extraction and gas chromatography with mass selective detection. *J. High Res. Chrom.* 18:221-225.
- KIMBALL, B. A., JOHNSON, D. L. NOLTE, and D. L. GRIFFEN. 1998a. Genetic control of constitutive terpenes in Douglas-fir vascular tissue. *For. Ecol. Mgmt.* Submitted.
- KIMBALL, B. A., D. L. NOLTE, R. M. ENGEMAN, J. J. JOHNSTON, and F. R. STREMITZ. 1998b. Chemically mediated foraging preferences of free ranging black bear (*Ursus americanus*). *J. Mammal.* 79:448-456.
- KIMBALL, B. A., D. L. NOLTE, D. L. GRIFFEN, S. M. DUTTON, and S. FERGUSON. 1998c. Impacts of live canopy pruning on the chemical constituents of Douglas-fir vascular tissues: implications for black bear tree selection. *For. Ecol. Mgmt.* In Print.
- KIMBALL, B. A., E. C. TURNBLOM, D. L. NOLTE, D. L. GRIFFEN, and R. M. ENGEMAN. 1998d. Effects of thinning and nitrogen fertilization on sugars and terpenes in Douglas-fir vascular tissues: implications for black bear foraging. *For. Sci.* Submitted.

- LANGSTROM, B., and C. HELLQVIST. 1991. Effects of different pruning regimes on growth and sapwood area of Scots pine. *For. Ecol. Manage.* 44:239-254.
- MASON, A. C., and D. L. ADAMS. 1989. Black bear damage to thinned timber stands in Northwest Montana. *West. J. Appl. For.* 4:10-13.
- NELSON, E. E. 1989. Black bears prefer urea-fertilized trees. *West J. Appl. Forest.* 4:13-15.
- NOBLE, W. O. 1993. Characteristics of spring foraging ecology among black bears in the central coast range of Oregon. Master's Thesis. Oregon State University, Corvallis, OR.
- O'HARA, K. L. 1991. A biological justification for pruning in coastal Douglas-fir stands. *West. J. Appl. For.* 6:59-63.
- RADWAN, M. A. 1969. Chemical composition of the vascular tissue of four tree species in relation to feeding by the black bear. *For. Sci.* 15:11-16.
- RADWAN, M. A., and W. D. ELLIS. 1975. Clonal variation in monoterpene hydrocarbons of vapors of Douglas-fir foliage. *For. Sci.* 21:63-67.
- REICHARDT, P. B., J. P. BRYANT, B. R. MATTES, T. P. CLAUSEN, F. S. CHAPIN III, and M. MEYER. 1990. Winter defenses of Alaskan balsam poplar against snowshoe hares. *J. Chem. Ecol.* 16:1941-1959.
- ROBBINS, C. T. 1983. *Wildlife Feeding and Nutrition*. Academic Press, Inc., Orlando, FL. 343 pp.
- SCHMIDT, W. C., and M. GOURLEY. 1992. Black bear. Pages 309-331 in *Silviculture Approaches to Animal Damage Management in Pacific Northwest Forests* (H. C. Black, ed.), USDA Technical Report PNW-GTR-287.
- STAND MANAGEMENT COOPERATIVE. 1993. Annual report. Stand Management Cooperative, College of Forest Resources, University of Washington, Seattle, WA.
- ZIEGLTRUM, G. J., and D. L. NOLTE. 1996. Black bear damage management in Washington State. *Proc. 7th East. Wildl. Dam. Manage. Conf.* 7:104-107.